A MITOCHONDRIAL DNA PERSPECTIVE ON THE HISTORICAL BIOGEOGRAPHY OF MIDEASTERN QUEENSLAND RAINFOREST BIRDS

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We approach the historical biogeography of the isolated mideastern Queensland (MQ) rainforests using mitochondrial DNA (mtDNA) phylogeography in three bird species present in rainforests of MQ, northeastern Queensland (NEQ) and southeastern Queensland and northeastern New South Wales (SE): the Large-billed Scrubwren *Sericornis magnirostris*, White-browed Scrubwren *S. frontalis* and Eastern Whipbird *Psophodes olivaceus*. We ask whether patterns of genetic diversity in these species, which we infer from restriction fragment length polymorphisms and sequence analyses, conform to a model of isolation by distance having operated prior to physical isolation of the NEQ, MQ and SE rainforests, or to a vicariance model whereby the dry woodland between Townsville and Bowen (the Burdekin Gap) first separated the NEQ rainforests from those of MQ and SE, which were isolated from each other later. In the Large-billed Scrubwren and Eastern Whipbird nucleotide diversities and sequence divergences are greatest in comparisons between NEQ and either SE or MQ or both, and phylogenetic analyses similarly cluster NEQ populations apart from those of MQ and SE. At the DNA sequence level in the cytochrome *b* gene, the strong sequence similarity (almost 100%) between SE and MQ populations of the Large-billed Scrubwren was especially noteworthy. These observations all suggest that the vicariance model has operated in these two species and that isolation of MQ rainforest from SE is much more recent than that of NEQ rainforests from MQ and SE. No clear trends were discernible in the White-browed Scrubwren and we attribute this to the species' high habitat plasticity, which, by facilitating gene flow, may have prevented the development of phylogeographic structure to mtDNA diversity. We further suggest that the biogeographical peculiarities of MQ rainforests (i.e. presence of a number of endemic species and subspecies coupled with the absence of other prominent rainforest endemics present in NEQ and SE rainforests) might be explained simply if MQ and SE rainforests have long been connected not by large tracts of unbroken rainforest but by scattered patches of a habitat such as vine thicket. ☐ *Rainforest, Sericornis, Psophodes, birds, mtDNA, historical biogeography, Queensland.*

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Of the rainforests scattered along Australia's eastern periphery (Fig. 1), those of mideastern Queensland (MQ) in the Mackay-Eungella-Clarke Range area are of particular biogeographic interest. Their affinities variously have been placed either with rainforests in northeastern Queensland (NEQ) (e.g. Schodde & Calaby, 1972) or, more often, with the subtropical rainforests of southeastern Queensland and northeastern New South Wales (SE, e.g. Webb & Tracey 1981; Cracraft, 1991). Although the MQ rainforests form a minor centre of endemism (Table 1), a number of taxa essentially confined to rainforest and present in rainforests to the north and south enigmatically are absent from them. Examples of the latter are the fig-parrots *Cyclopsitta* spp., logrunners *Orthonyx* spp., riflebirds *Ptiloris* spp., catbirds *Ailuroedus* spp., and Yellow-throated Scrubwren *Sericornis citreogularis*;and among the skinks *Coeranoscincus* spp. Further interest derives from some species complexes having isolated populations in MQ rainforest and other populations in SE or NEQ or both. Analyses of morphological variation in some of these (e.g. Boles, 1983 for the Brown Thornbill, *Acanthiza pusilla*), suggest some MQ isolates are more closely related to SE populations than to those of geographically closer NEQ. In other complexes having undifferentiated MQ isolates there are clear affinities with NEQ (e.g. the skinks *Saproscincus basilicus* and *Carlia rhomboidalis*) or with SE (e.g. the skink *Lampropholis delicata* – Mather, 1990; Mather & Hughes, 1992). Still other MQ isolates are of uncertain affinity because they are morphologically intermediate between conspecifics in north-

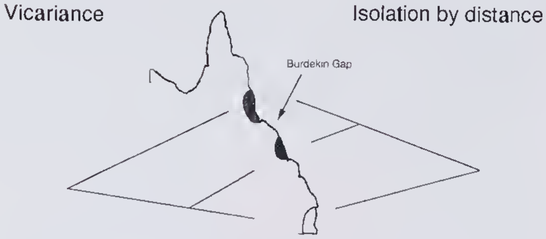

FIG. 1. Location of mideastern Queensland rainforests, their isolation from rainforests of northeastern Queensland and south-central eastern Australia, and the location of the Burdekin Gap. Superimposed on this are the two models of phylogenetic relationships among populations of species inhabiting rainforests tested here.

eastern and southeastern Queensland (e.g. Boles & Longmore, 1983 for the White-throated Treecreeper *Cormobates leucophaea intermedia*). Molecular analyses bearing on phylogenetic affinities of MQ populations at present are few and limited in extent (e.g. Christidis & Schodde, 1991).

Given these observations and analyses, we chose to investigate the historical biogeography of MQ rainforest birds and the evolutionary connections between populations in MQ, SE and NEQ rainforests. We have used an approach that integrates phylogenetic and geographical patterns of diversity in mitochondrial DNA (mtDNA). Such patterns are increasingly being used to explore interactions between phylogeny, ecology and biogeography. Mitochondrial DNA is well-suited to this type of analysis for reasons that have been discussed by a number of authors (Avise et al., 1987; Moritz et al. 1987). Analyses of mtDNA can be used to trace within-species phylogenetic patterns and to place them in the context of a species' geographical distribution. This has created a bridge between systematics and population genetics that Avise et al. (1987) called intraspecific phylogeography, and which we are using to analyse the biogeographical history of NEQ rainforests (e.g. Moritz et al., 1993). Phylogeography has also been used to interpret the biogeographical history of several species assemblages and faunas in the United States (Bermingham et al., 1992; Lamb et al., 1992; Avise, 1992).

From palynological and climatological analyses, it has been established that rainforest fluctuated in extent at specific sites in eastern Australia during the Pleistocene, with eucalypt-dominated habitats replacing rainforest for periods of several thousands of years (e.g. Walker, 1990; Kershaw, 1986). Less clear are the dynamics of rainforest's extent on the broader geographical scale in eastern Australia, although rainforest is known to have extended well into southeastern Australia during the Tertiary (Truswell, 1990). In this paper we test hypotheses concerning the presence and absence of connections among rainforests of MQ, SE and NEQ by examining mtDNA phylogeography of birds inhabiting those rainforests (Fig. 1). Notwithstanding what might be considered the null hypothesis of there being no geographical structure in within-species mtDNA diversity, we ask whether geographical patterns of mtDNA diversity in these species reflect either the effects of isolation by distance prior to the isolation of the NEQ, MQ and SE populations, or historical effects of vicariance induced by the dry, sparsely wooded corridor between Townsville and Bowen (the Burdekin Gap — Ford, 1986; Winter, 1984; Galbraith, 1969). In applying an isolation by distance model to a continuously distributed species with limited dispersal, one expects that the degree of genetic differentiation between two individuals will increase with increasing distance between the sites of sampling. Under this model, we would expect MQ populations to have closest phylogenetic affinity with populations geographically closest to them (i.e. those from NEQ). Under a vicariance model, MQ populations would be expected to be closer to SE populations if the Burdekin Gap has operated for an evolutionarily long period.

We focus on three bird species that occur in MQ, SE and NEQ rainforests: Large-billed Scrubwren, *Sericornis magnirostris*, White-browed Scrubwren, *S. frontalis* and Eastern Whipbird, *Psophodes olivaceus*. Populations of the Large-billed Scrubwren in the three areas are isolated from one another with the NEQ birds recognized as *S. m. viridior* due to minor differentiation in plumage (Christidis et al., 1988). The White-browed Scrubwren is continuously distributed between NEQ and SE rainforests and its NEQ populations have been separated as *S. f. herbertoni* although this subspecies is not currently recognized (Christidis & Schodde, 1991; Ford, 1985; Storr, 1984). The NEQ populations of the Eastern Whipbird are geographically isolated and recognized as *P. o. lateralis* (Blakers et al., 1984; Storr, 1984). All three species occur in a range of forested habitats. The Large-billed Scrubwren and Eastern Whipbird favour rainforest and wetter temperate forests, whereas the White-browed Scrubwren is far less specialized,

MQ endemic taxa	Presumed closest relative(s)	Distributions	Reference
Mammals			
*Petrogale persephane**	?*P. xanthapus*	inland SE Australia	Maynes, 1982; Edridge et al., 1992
Birds			
Meliphaga hindwoodi	*M. chrysops**	SE Australia (non-breeding migrant to NEQ)	Longmore & Boles, 1983
	M. frenata	NEQ	Longmore & Boles, 1983
Acanthiza pusilla mcgilli	*A.p. pusilla*	SE Australia	Boles, 1983
Carmobates leucaphaea intermedia	?*C.l. leucaphaea*	SE Australia	
Reptiles			
Phyllurus spp. (*caudiannulatus, isis, nepthys, assa*)	*P. platurus**	Hawkesbury sandstone, NSW	Couper et al., 1993
Eulamprus amplus	?	–	
E. luteilateralis	*E. murrayi*	SEQ, NE NSW	Covacevich & McDonald, 1980
*Lygisaurus zuma**	?	–	Couper, 1993
*Anomalapus brevicollis**	*A. gawi**	NEQ	Greer & Cogger, 1985
Amphibians			
Rheobatrachus vitellinus	*R. silus*	SEQ	Mahony et al., 1984
Taudactylus eungellensis	*T. diurnus*	SEQ	Ingram, 1980
T. liemi	?	–	Ingram, 1980

TABLE 1. Summary table of taxa endemic to mideastern Queensland with presumed closest relatives and their distributions. See Stanisic (1990) and Dyne (1991) for some invertebrate groups. An * indicates a species not normally found in rainforest.

occurring also in shrubby undergrowth in drier areas (Crome, 1990, table 1).

MATERIALS AND METHODS

RESTRICTION SITE ANALYSIS

Restriction endonucleases are used to sample nucleotide sequence variation. Information from several restriction enzymes is combined to define different alleles or 'haplotypes' of mtDNA present in different individuals. We have described the method in more detail elsewhere (Dowling et al., 1990; Joseph & Moritz, 1993a). Our comparisons are based on mapped or unambiguously inferred restriction sites, mostly using enzymes that recognize sequences of six bases, and extend our previous analyses of restriction site variation (Joseph & Moritz, 1993b). In addition, we present new evidence from DNA sequences.

From a survey of restriction fragment length polymorphism (RFLP) of the entire mtDNA genome in each species we derive proportions of shared restriction sites and from these obtain sequence divergence estimates within and among individuals from NEQ, MQ and SE populations by the maximum likelihood method of Nei & Tajima (1983). Nucleotide diversity, a measure of the average difference between any two mtDNAs, was derived either with the the REAP package of McElroy et al. (1992) using the GENERATE, D and DA functions, or calculated manually (e.g. Quinn & White, 1987); nucleotide diversity values in comparisons between two populations have been corrected for within-population variation. Phylogenetic relationships among haplotypes in the three populations were derived from the same data using parsimony from PAUP Version 3.0s (Swofford, 1991) and MacCLADE Version 3 (Maddison & Maddison, 1992). The significance of branching points was assessed with 500 randomized replicates using the exhaustive search option of PAUP. Hedges (1992) urged that a minimum of 2,000 replicates be performed unless computing time is prohibitive. In view of this and with reference to Fig. 1 of Hedges (1992), we contend that given the relatively simple data sets obtained here with small numbers of taxa, 500 replicates are adequate.

DNA SEQUENCING

Next, we sought finer resolution of the patterns obtained from RFLP with direct sequencing of approximately 270 bp of the cytochrome *b* gene using templates generated by the polymerase chain reaction (PCR). To minimize the chance of amplifying nuclear DNA copies of mtDNA sequences, most sequences (23 of 29) were amplified from mtDNA that had been purified by ultracentrifugation in a CsCl density gradient (Dowling et al., 1990); one outgroup sequence, that of the Grey-crowned Babbler, *Pomatostomus temporalis*, was obtained from the literature. The

TABLE 2. Numbers of individuals examined by RFLP and sequence analysis for three species studied and in three rainforest blocks NEQ, MQ and SE of eastern Australia. South-east* indicates southeastern Queensland and northeastern New South Wales. Locality details for the scrubwren samples are in Joseph & Moritz (1993a, b) and voucher specimens of the scrubwrens are held mostly in the Queensland Museum, Brisbane. For the whipbird samples, details of collection localities and field identification numbers of specimens used in RFLP analysis are in the caption to Table 4. The following were used for sequence analysis: SE: L 226, C 291, Ps 1; MQ: C 529; NEQ:C 564, Ps 7 (Atherton Tableland). All whipbird specimens are lodged with the Australian National Wildlife Collection, Canberra or Museum of Victoria, Melbourne except Ps 1, which is lodged at the Queensland Museum. Only a blood sample was available from Ps 7.

	Restriction Fragment Length Polymorphism Analysis			*Cytochrome b* Sequence Analysis		
	North-east Queensland	Middle Eastern Queensland	South-east*	North-east Queensland	Middle Eastern Queensland	South-east*
Large-billed Scrubwren *Sericornis magnirostris*	15	3	9	6	3	3
White-browed Scrubwren *S. frontalis*	3	2	10	3	4	2
Eastern Whipbird *Psophodes olivaceus*	1	1	6	2	1	3

six samples obtained by PCR amplification of total cellular DNA were AQ 8, SK 14, SF 35, SF 37, Ps 7 and SM 111 and these showed no signs of involving a nuclear copy. The initial PCR involved 30 cycles of denaturing at 93°C for 35s, annealing at 48°C for 1 m and extension at 72°C for 1 m. PCR products were then purified and sequences obtained by cycle sequencing (Murray 1989; 25 cycles of denaturing at 94°C, annealing at 58°C and extension at 70°C, each for 30 secs) using only minor modifications of the commercially available BRL kit. Primers used were based on those of Kocher et al. (1989) and were:

Light strand:
`cyt b1: 5'- TACCCGGGGATCCCCATCCAACATCT-CAGCATGATGAAA - 3'`

Heavy strand:
`cyt b2: 5' - CCGGATCCCCGGCCCTCAGAATGAT-ATTTGTCCTCA - 3'`

Sequences initially were obtained from both strands in at least one individual for each species from NEQ, MQ and SE. Subsequent sequencing was done only on the light strand except to verify further polymorphisms where necessary.

For sequence analyses, we used any further MQ samples available and, if possible, at least five individuals from SE and NEQ (Table 2). Sequence divergences were calculated by direct count and nucleotide diversities calculated and phylogenetic analyses done as for the RFLP data. Most methods are described in Hillis & Moritz (1990).

RESULTS

For the scrubwrens we present a summary of RFLP data, most of which have been presented in full in Joseph & Moritz (1993b). For the whipbird and all sequence analyses we offer more complete presentations.

LARGE-BILLED SCRUBWREN

Previous RFLP analyses revealed one common haplotype in northeastern Queensland (present in 8 of 15 individuals surveyed) with several other very similar haplotypes (sequence divergences 0.2% ± 0.2 to 0.7% ± 0.4) separated from it by small numbers of site changes. A similar situation applied to SE samples. Sequence divergence between SE and NEQ samples ranged from 1.2 ± 0.6 to 1.7 ± 0.7% but inclusion of further restriction sites not considered in the earlier study saw the divergences rise (e.g. to 2.2% ± 0.6 between the most common SE and NEQ haplotypes). All three MQ individuals had the same haplotype, which differed by 0.8 ± 0.5% from the common SE haplotype and by 2.6 ± 0.8% from the common NEQ one. Nucleotide diversities showed a similar pattern with the values in comparisons between NEQ and either MQ or SE (0.021 in both) being up to an order of magnitude greater than between SE and MQ or within either NEQ, MQ or SE (Table 3). Together, these values indicate that mtDNA diversity in this species was most strongly structured geographically between NEQ on one hand and MQ/SE on the other. The phylogenetic analysis of Joseph & Moritz (1993b), designed to investigate relationships between species of *Sericornis*, was extended to study the phylogenetic structure within this species by including all SE haplotypes and the

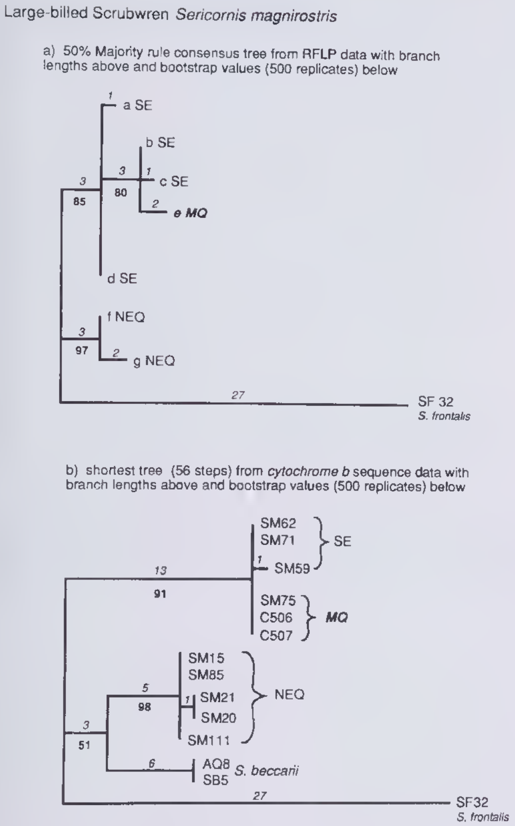
Large-billed Scrubwren *Sericornis magnirostris*
a) 50% Majority rule consensus tree from RFLP data with branch lengths above and bootstrap values (500 replicates) below
1
a SE
b SE
3
1
c SE
3
80
85
2
e MQ
d SE
f NEQ
3
97
2
g NEQ
27
SF 32
S. frontalis
b) shortest tree (56 steps) from *cytochrome b* sequence data with branch lengths above and bootstrap values (500 replicates) below
SM62
SM71
SE
1
SM59
13
91
SM75
C506
MQ
C507
SM15
SM85
5
1
SM21
NEQ
98
SM20
3
SM111
51
6
AQ8
SB5
S. beccarii
27
SF32
S. frontalis

FIG. 2. Trees produced from analysis of RFLP (a) and sequence data (b) in the Large-billed Scrubwren showing bootstrap values and branch lengths. Though not central to the aims here, the Tropical Scrubwren *S. beccarii* has been included. Its position in the analysis reinforces the findings of Joseph & Moritz (1993b). The letters a to g in (a) correspond to the haplotypes shown in Appendix 1.

White-browed Scrubwren as an outgroup (Appendix 1). In a 50% majority rule consensus tree (42 steps in length), the MQ haplotype consistently clustered with all SE ones (85% of 500 randomized pseudoreplicates) and the two NEQ haplotypes aligned with each other (97% of 500 pseudoreplicates) (Fig. 2a). This provided a better explanation for six characters when compared with a tree constrained to place MQ with NEQ; the latter better explained only one character and was five steps longer.

Sequence for the cytochrome *b* gene was obtained from 12 individuals all of which except one (SM 111) had also been assayed for RFLP. 279 bp were sequenced in most individuals with a minimum of 256 bp (Fig. 3). Nineteen nucleotide sites were polymorphic. NEQ individuals were polymorphic at one third codon position and the SE and MQ individuals were identical except for one site change present in a single SE individual. Together, the MQ/SE individuals were 6.9% divergent from the common NEQ sequence. Nucleotide diversities showed a similar pattern with the diversities for the comparisons between NEQ and either MQ or SE being an order of magnitude greater than all other comparisons within and among populations (Table 3). Phylogenetic analysis of the cytochrome *b* sequence data, which included the White-browed Scrubwren as an outgroup, emphasized the close relationship between MQ and SE individuals suggested from RFLP patterns (Fig. 2b). In the shortest tree (56 steps) all SE and MQ individuals clustered together and apart from all north-eastern individuals. Among the NEQ individuals, SM 20 and 21 were united by a shared site change but SM 111 separated because of uncertain base assignment at one site. This tree was 12 steps shorter than the shortest tree that could be produced under the constraint of MQ and NEQ individuals being monophyletic. It provided significantly better explanations for twelve characters compared with zero better explained by the constrained tree (chi-squared = 12, *d.f.* = 1, $p < 0.001$).

WHITE-BROWED SCRUBWREN

In a previous RFLP analysis (Joseph & Moritz, 1993b), MQ, SE and NEQ haplotypes essentially formed a single cluster with sequence divergences mostly 0.5% or less and nucleotide diversities consistently low (< 0.003) in all comparisons within and among populations (Table 3). The relationships of the common SE haplotype and single NEQ and MQ haplotypes were poorly resolved (Joseph & Moritz, 1993b). Further analysis using an additional five haplotypes defined by RFLP from 14 restriction endonucleases, and with the Atherton Scrubwren, *S. keri* as an outgroup, still could not produce a well resolved phylogeny in this species (data not shown).

In sequence analyses, 276 bp were obtained with a minimum of 238 bp (Fig. 4). Only five nucleotide sites varied and all base changes were silent transitions at third base positions. Sequence divergences ranged from zero between SF 5 from NEQ and all MQ samples, to 1.2% between SF 3 and SF 30 from NEQ and SE, respectively. Nucleotide diversities were also low in all com-

	Within SE	Within NEQ	SE-MQ	NEQ-MQ	SE -NEQ
Large-billed Scrubwren					
RFLP	0.006 (8)	0.003 (15)	0.004 (11)	0.021 (18)	0.021 (22)
cyt b	0.003 (3)	0.003 (5)	0.000 (6)	0.030 (8)	0.037 (8)
White-browed Scrubwren					
RFLP	0.002 (10)	0.00 (3)	0.003 (12)	0.002 (6)	0.001 (13)
cyt b	0.016 (2)	0.015 (3)	0.000 (6)	0.001 (7)	0.000 (5)
Eastern Whipbird					
RFLP	0.007 (6)	0.00 (1)	0.009 (7)	0.028 (2)	0.009 (7)
cyt b	0.011 (3)	0.01 (2)	0.004 (4)	0.009 (3)	0.0054 (5)

TABLE 3. Nucleotide diversities estimated from RFLP and sequence data within and among populations of NEQ, MQ and SE for the three species. Sample sizes are shown in brackets. Values shown for between population comparisons have been corrected for within-population diversity.

Large-billed Scrubwren *Sericornis magnirostris cytochrome b* sequence starting from position 14862 relative to the complete human mtDNA sequence

NEQ a - north-eastern Queensland, individuals SM 20, 21
NEQ b - north-eastern Queensland, individuals SM 15, 85, 111
MQ - middle eastern Queensland, individuals SM 75, C506, C507
SE a - south-eastern Queensland, individuals SM 62, 71
SE b - south-eastern Queensland, individual SM 59

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                    Ile Cys Leu Met Thr Gln Ile Ile Thr Gly Leu Leu Leu Ala Met His Tyr Thr
NEQ a               ATC TGC CTA ATA ACT CAA ATC ATC ACA GGC CTC CTG CTA GCC ATA CAC TAC ACG
NEQ b               ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
MQ                  ..T ... ... ... ... ... ... ... ... ... ... ..A ... ... .C. ... ... ..A
SE a                ..T ... ... ... ... ... ... ... ... ... ... ..A ... ... .C. ... ... ..A
SE b                ..T ... ... ... ... ... ... ... ... ... ... ..A ... ... .C. ... ... ..A


        Ala Asp Thr Thr Leu Ala Phe Ser Ser Val Ala His Met Cys Arg Asn Val Gln Phe Gly Trp
NEQ a   GCA GAC ACT ACA CTA GCC TTC TCC TCT GTC GCT CAT ATA TGC CGA AAC GTC CAA TTC GGC TGA
NEQ b   ... ... ... ..C ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
MQ      ..G ... ..C ..C ... ... ..T ... ..C ... ... ... ..G ... ... ... ... ... ... ... ...
SE a    ..G ... ..C ..C ... ... ..T ... ..C ... ... ... ..G ... ... ... ... ... ... ... ...
SE b    ..G ... ..T ..C ... ... ..T ... ..C ... ... ... ..G ... ... ... ... ... ... ... ...


        Leu Ile Arg Asn Leu His Ala Asn Gly Ala Ser Phe Phe Phe Ile Cys Ile Tyr Leu His Ile
NEQ a   CTC ATC CGC AAC CTC CAT GCA AAC GGG GCT TCA TTC TTC TTT ATC TGC ATC TAC CTT CAC ATC
NEQ b   ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
MQ      ... ... ... ... ... ..C ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SE a    ... ... ... ... ... ..C ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SE b    ... ... ... ... ... ..C ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...


        Gly Arg Gly Phe Tyr Tyr Arg Ser Tyr Leu Asn Lys Glu Thr Trp Asn Val Gly Val Ile Leu
NEQ a   GGA CGA GGA TTC TAC TAC GGC TCC TAC TTG AAC AAA GAA ACC TGA AAC GTC GGA GTT ATC CTC
NEQ b   ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
MQ      ... ... ... ... ... ... ... ... ... C.A ... ... ... ... ... ..T A.. ..G ... ... ...
SE a    ... ... ... ... ... ... ... ... ... C.A ... ... ... ... ... ..T A.. ..G ... ... ...
SE b    ... ... ... ... ... ... ... ... ... C.A ... ... ... ... ... ..T.A.. ..G ... ... ...


        Leu Leu Ala Leu Met Ala Thr Ala Phe Val Pro Met
NEQ a   CTC CTG GCC CTT ATA GCA ACT GCT TTC GTA CCT ATG
NEQ b   ... ... ... ... ... ... ... ... ... ... ... ...
MQ      ... ..A A.T ... ... ... ...
SE a    ... ..A A.T ... ... ... ... ...
SE b    ... ..A A.T ... ... ... ...
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FIG. 3. Sequence of part of the cytochrome *b* gene in the Large-billed Scrubwren in individuals from NEQ, MQ and SE. In this and Figs 4 and 7, the amino acid sequence is included for the purposes of a) verifying that true mtDNA sequence and not non-functional nuclear copies have been obtained and b) making the amino acid sequence itself available for any subsequent phylogenetic analyses at that level.

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White-browed Scrubwren Sericornis frontalis cytochrome b sequence starting from position 14855
relative to the complete human mtDNA sequence


                        Leu Gly Ile Cys Leu Met Thr Gln Ile Ile Thr Arg Leu Leu Leu Ala Met His Tyr Thr
SF 3 NEQ              A CTA GGT ATC TGC CTA ATA ACT CAA ATC ATC ACA GGC CTT CTA CTG GCC ATA CAC TAC ACA
SF 4 NEQ                                                        ... ... ... ... ... ... ... ... ... ...
SF 5 NEQ                                                        ... ... ... ... ... ... ... ... ... ...
SF 32 MQ                                                        ... ... ... ... ... ... ... ... ... ...
SF 33 MQ                              . ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 35 MQ                              . ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 37 MQ                              . ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 2  SE                                                        ... ... ... ... ... ... ... ... ... ...
SF 30 SE              . ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ..T ... ...

                    Ala Asp Thr Thr Leu Ala Phe Ser Cys Val Ala His Met Cys Arg Asn Val Gln Phe Gly Trp
SF 3 NEQ            GCA GAC ACC ACC CTA GCT TTC TCT TCC GTT GCC CAC ATA TGC CGA AAC GTC CAA TTT GGC TGA
SF 4 NEQ            ... ... ... ... ... ... ... ..C ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 5 NEQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 32 MQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 33 MQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 35 MQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 37 MQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 2  SE            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 30 SE            ... ... ... ... ... ... ... ..C ... ... ... ... ... ... ... ... ... ... ... ... ...

                    Leu Ile Arg Asn Leu His Ala Asn Gly Ala Ser Phe Phe Phe Ile Cys Ile Tyr Leu His Ile
SF 3 NEQ            CTT ATC CGC AAC CTT CAC GCA AAC GGA GCC TCA TTC TTT TTT ATC TGC ATC TAC CTC CAC ATC
SF 4 NEQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 5 NEQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 32 MQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 33 MQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 35 MQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .
SF 37 MQ            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 2  SE            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 30 SE            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...

                    Gly Arg Gly Phe Tyr Tyr Gly Ser Tyr Leu Asn Lys Glu Thr Trp Asn Val Gly Val Ile Leu
SF 3 NEQ            GGA CGG GGC TTT TAC TAC GGC TCC TAC CTA AAC AAA GAA ACC TGA AAC GTC GGA GTA ATC CTC
SF 4 NEQ            ..G ... ... ..C ... ... ..T ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 5 NEQ            ..G ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 32 MQ            ..G ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ..
SF 33 MQ            ..G ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 37 MQ            ..G ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .
SF 2  SE            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SF 30 SE            ..G ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...


                    Leu Ser Ser Pro His Ser Asn Cys Leu
SF 3 NEQ            CTC TCT AGC CCT CAT AGC AAC TGC CTT
SF 4 NEQ            ... ... ... ... ... ... ... ..
SF 5 NEQ            ... ... ... ... ... ... ... ..
SF 33 MQ            ... ... ..
SF 2  SE            ... ... ... ... ... ... ... ..
SF 30 SE            ... ... ... ... ... ... ... ... ...
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FIG. 4. Sequence of part of the cytochrome *b* gene in the White-browed Scrubwren in individuals from NEQ, MQ and SE.

parisons within and among populations reaching 0.01 only within NEQ and within SE. As was the case with RFLP analysis, phylogenetic analysis of the small number of informative sites in the sequence data showed no consistent pattern of relationships among the three areas SE, MQ and NEQ (Fig. 5).

Eastern Whipbird

In the RFLP analysis, between 46 and 51 sites unambiguously were inferred after digesting the mtDNA genomes with the same 17 restriction endonucleases as used for *Sericornis* (Appendix 2, Table 4). The MQ sample was identical with one from southeastern Queensland, both of which in turn were very similar to the individuals from New South Wales (sequence divergences 0.2 ± 0.2% to 1.1 ± 0.4%). In contrast, in comparisons between MQ/SE and the individual from NEQ divergences reached between 2.5 ± 0.7% and 2.8 ± 0.8% (Table 5). Nucleotide diversities suggested a similar pattern, being 0.007 within SE (only single individuals were available from MQ and NEQ) and 0.009 between MQ and SE but 0.028 in comparisons between MQ and NEQ and 0.009 between SE and NEQ (Table 3). Structuring of mtDNA diversity in the limited sample of this species was most strongly suggested between NEQ and MQ/SE combined. No RFLP data were available for use as an outgroup in phylogenetic analysis for this species so an unrooted phylogenetic network linking all haplotypes was constructed using only unambiguous characters (Fig. 6a). In a tree 21 steps in length the single NEQ individual was on a branch separate from all other samples while those from south-eastern and middle eastern Queensland, which were the same haplotype, were aligned with one of the New

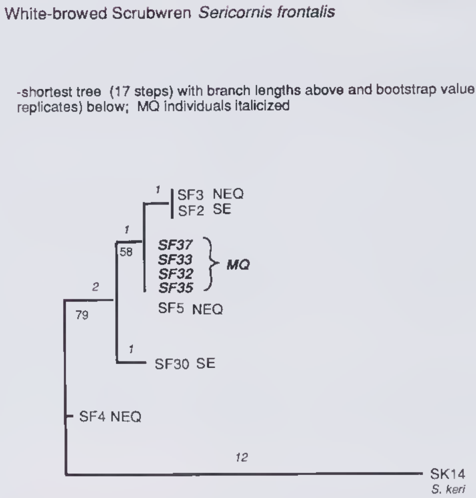
White-browed Scrubwren *Sericornis frontalis*
-shortest tree (17 steps) with branch lengths above and bootstrap values (500 replicates) below; MQ individuals italicized
1
SF3 NEQ
SF2 SE
1
58
SF37
SF33
SF32
SF35
MQ
2
79
SF5 NEQ
1
SF30 SE
SF4 NEQ
12
SK14
S. keri

FIG. 5. Tree produced from analysis of sequence data in the White-browed Scrubwren showing bootstrap values and branch lengths.

South Wales samples. Placing MQ with NEQ produced a tree one step longer that better explained only one character compared with two better explained in the tree aligning MQ with SE.

In sequence analyses, up to 264 bp were sequenced in six individuals with a minimum of 228 bp (Fig. 7). Seven nucleotide sites varied across NEQ, MQ and SE. Among all the MQ and SE individuals, divergence ranged from zero (between C529 and Ps 1 from middle eastern and south-eastern Queensland, respectively) to 0.9% and 1.1% in comparisons among SE individuals. Between SE/MQ and NEQ individuals divergences ranged from 1% to 3% while divergence between the two NEQ individuals was 0.9%. Nucleotide diversities weakly suggested structuring to the diversity with between population values being generally lower than those within populations but with the highest value being in the NEQ-MQ comparison (Table 3). Though few phylogenetically informative characters were available, phylogenetic analysis was done using sequence from the Grey-crowned Babbler (Edwards et al., 1991) as an outgroup. A shortest tree 33 steps in length was produced that grouped the two NEQ individuals apart from all SE and MQ individuals (Fig. 6b). Placing the single MQ individual with NEQ did not better explain any characters and resulted in a tree two steps longer.

DISCUSSION

mtDNA PHYLOGEOGRAPHY

To shed light on the historical biogeography of MQ rainforests we have looked at the phylogeographic structure of mtDNA diversity in three bird species common to MQ, SE and NEQ rainforests and asked whether the structures are consistent with isolation by distance or vicariance models. The patterns revealed by RFLP and sequence analyses in the three species in general were concordant in that where geographic structuring was present, the patterns were the same. In this regard, the identity between MQ and SE individuals at the sequence level in the Large-billed Scrubwren was striking, although RFLP assays did reveal some variation in other parts of the mtDNA genome. These patterns strongly suggest that in the Large-billed Scrubwren and, to a lesser extent the Eastern Whipbird, mtDNA diversity is apportioned between SE and MQ populations on one hand and NEQ on the other. For these two species, we can favour the hypothesis of a vicariance event about the Burdekin Gap having isolated MQ and SE populations from NEQ ones. If isolation by distance has operated in these species, then its effects are minor compared with those of vicariance induced by the Burdekin Gap. This in turn implies that the Burdekin Gap has been a long-standing biogeographical barrier, a conclusion consistent with geographical patterns of morphological variation as expressed in existing subspecific taxonomy in these two species.

In the White-browed Scrubwren, however, there was no clear geographic structure despite substantial variation in RFLP analyses and the phylogenetic relationships among the mtDNA alleles seem poorly resolved; the greatest divergence was between some SE haplotypes. The situation in this species is consistent with neither the isolation by distance nor the vicariance model and we suggest that this species has not evolved a stable phylogeographic structure in mtDNA diversity among its Queensland populations; the situation is at present less clear with regard to morphological diversity (Ford, 1985). This may be attributable to the species' far greater habitat diversity relative to the other two species studied, as this probably facilitates rapid and widespread dispersal. Christidis & Schodde (1991) argued from allozyme data that a zone of secondary intergradation in the White-browed Scrubwren occurs about the latitude of Rockhampton, which is south of the MQ rainforests. Unfortunately,

	Ava I	*Bam HI*	*Bcl I*	*Bgl II*	*Dra I*	*Eco 0109*	*Eco RI*	*Eco RV*	*Hind III*	*Nco I*	*Nhe I*	*Pvu II*	*Spe I*	*Hinp I*	*Hinf I*	*Msp I*
New South Wales																
D750	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
L226	.	.	.	.	?	.	.	.	.	.	.	?	.	.	.	.
L255	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.
B840	.	.	.	.	B	B	.	.	.	B	.	B	.	.	.	B
C291	.	.	.	.	B	B	.	.	.	B	.	B	.	.	.	B
South-East Queensland																
Ps I	.	B	B	.	B	B	.	.	.	C	.	.	B	A?	A?	A?
Middle Eastern Queensland																
C529	.	B	B	.	B	B	.	.	.	C	.	.	B	–	A?	?
North-East Queensland																
C564	.	B	C	B	C	C	B	.	C	D	B	C	C	B	A?	C

D750: Nowra, NSW
L226: Kiola, NSW
L255: Kangaroo Valley, NSW
B840: Cambridge Plateau, NSW
C291: Mebbin State Forest, NSW
Ps 1: Conondale Ranges, South-East Queensland
C529: Cathu State Forest, Middle Eastern Queensland
C564: Mission Beach, North-East Queensland

TABLE 4. Restriction fragment profiles in the Eastern Whipbird. Question marks indicate uncertain typings.

they were only able to analyse NEQ populations for one locus (*AlD*) and further analysis of allozymes in northeastern Queensland populations would be desirable.

The mtDNA data, then, provide a basis for suggesting that isolation of the MQ and SE rainforests from each other is very recent compared with that of the NEQ rainforests from those of SE and MQ. Further, we may conclude that vicariance induced by the Burdekin Gap has been a major force in shaping patterns of genetic diversity within rainforest birds such as the Large-billed Scrubwren and Eastern Whipbird as well as in shaping species distributions. The White-browed Scrubwren, however, is a species for which mtDNA diversity and geographical range appear not to have been so affected; its broader habitat range and likely greater dispersal abilities may act to override the evolution of any phylogeographic structure.

SPECULATIONS ON MQ BIOGEOGRAPHY

The mtDNA evidence indicates recent connections between SE and MQ rainforests. These connections could have been either of two types: (i) continuous tracts of rainforest only recently broken into present disjunct isolates or, (ii)scattered patches of a habitat such as vine thickets or dry rainforest that could have existed for much of the Pleistocene. Either interpretation would be consistent with the patterns of genetic diversity we have reported here, but the second is more consistent with both the absence in MQ of several highly specialized rainforest species of SE and NEQ rainforests, and the presence of less specialized species such as we have studied here in each of SE, MQ and NEQ rainforests. Further, the lack of substantial rainforest connections could have promoted the evolution of MQ rainforest endemics (Table 1). What remains to be explained is the initial absence from MQ of several rainforest species found in both NEQ and SE rainforests. As suggested by Winter (1988) to explain the dearth of rainforest specialists among the mammals of SE rainforests, it could be that MQ rainforests contracted to an area too small to support obligate rainforest species during the driest period of the Pleistocene glacials. However, the absence of the Yellow-throated Scrubwren *S. citreogularis*, a species now capable of occupying wet sclerophyll as well as rainforest habitats, remains difficult to understand. The mtDNA divergence between the SE and NEQ populations is at least as great as that between those of the Large-billed Scrubwren (Joseph & Moritz, 1993b) so they might be expected to have reacted similarly to habitat changes and vicariance events.

A prediction from the second suggestion is that the endemic species of MQ rainforests are des-

	D 750, L 226 (NSW)	L 255 (NSW)	B 840, C 291 (NSW)	Ps 1 (SE Qld), C 529 (MQ)	C 564 (NEQ)
D 750, L 226 (NSW)	49	48	46	47	41
L 255 (NSW)	0.2 ± 0.2	48	45	46	40
B 840, C 291 (NSW)	0.9 ± 0.4	1.1 ± 0.4	48	47	40
Ps 1 (SE Qld), C 529 (MQ)	1.0 ± 0.4	1.2 ± 0.4	0.9 ± 0.4	51	41
C 564 (NEQ)	2.5 ± 0.7	2.7 ± 0.8	2.7 ± 0.8	2.8 ± 0.8	46

TABLE 5. Matrix of sequence divergence values between different haplotypes in the Eastern Whipbird. Numbers of sites inferred in each haplotype are on the leading diagonal, while numbers of shared sites and sequence divergence values and their standard deviations are above and below the diagonal, respectively.

cendants of lineages that were either capable of surviving in small rainforest patches or that were non-rainforest forms. This could be tested by placing habitat preference of MQ endemics, especially the most narrowly distributed ones with rainforest specialization, and their close relatives in a framework of the phylogenetic affinities among the species themselves. One could then argue whether habitat shifts from eucalypt to rainforest have occurred and, if so, whether MQ rainforest endemics are likely derived from non-rainforest inhabiting ancestral lineages. The leaf-tailed geckoes *Phyllurus* spp., which include narrowly distributed rainforest endemics in MQ and other species showing varying degrees of dependence on rainforest, are an example of such a group (Couper et al., 1993). The Eungella Honeyeater of MQ rainforests (Table 1) would provide a further useful test as its closest relative is either the Yellow-faced Honeyeater *M. chrysops* of eastern Australian eucalypt forests or the Bridled Honeyeater *M. frenata* endemic to NEQ rainforests (Longmore & Boles, 1983). Habitat shifts from rainforest to eucalypt habitats have long been considered to have been involved in the evolution of the Australian biota but the reverse has rarely, if ever, been proposed. MQ rainforests provide an opportunity to test for such shifts.

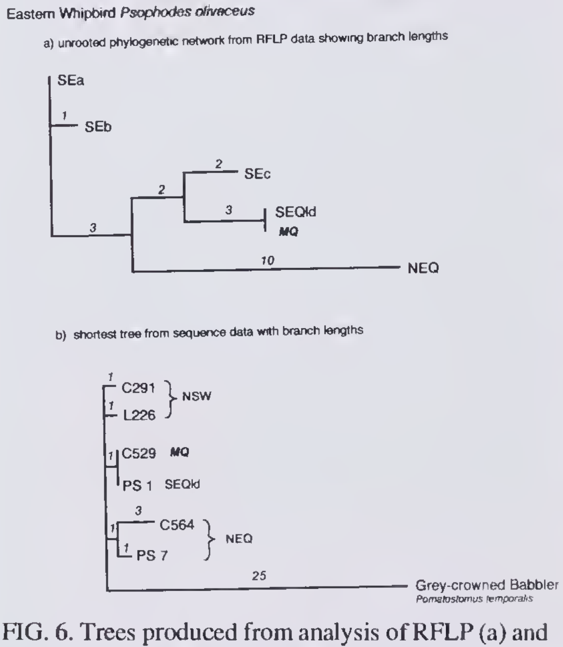
Eastern Whipbird *Psophodes olivaceus*
a) unrooted phylogenetic network from RFLP data showing branch lengths
SEa
1
SEb
2
SEc
2
3
SEQld
MQ
3
10
NEQ
b) shortest tree from sequence data with branch lengths
1
C291
1
L226
NSW
1
C529
MQ
PS 1
SEQld
3
1
C564
1
PS 7
NEQ
25
Grey-crowned Babbler
Pomatostomus temporalis

FIG. 6. Trees produced from analysis of RFLP (a) and sequence data (b) in the Eastern Whipbird to show bootstrap values and branch lengths. The letters a to c in (a) correspond to the haplotypes shown in Appendix 2.

The existence between MQ and SE of a number of very narrowly distributed species endemic to small, isolated patches of rainforest and wetter forest types would be consistent with long-term habitat connections between MQ and SE rainforests having been through scattered habitat patches rather than continuous rainforest. Examples are especially prominent in the Kroombit Tops region from where the day frog *Taudactylus pleione* Czechura, 1986 and a number of charopid land snails (Stanisic, 1990) are known. The recently discovered and most distinctive scincid genus *Nangura* from near Murgon (Covacevich et al., 1993) is a further example.

In conclusion, we submit that mtDNA intraspecific phylogeography offers increased resolution over that available so far in studies of the historical biogeography of middle eastern Queensland rainforests. However, more insight may be forthcoming from the other species listed in Table 1. Phylogenetic analyses of groups with narrowly distributed MQ endemics (e.g day frogs

```
Eastern Whipbird Psophodes olivaceus cytochrome b sequence starting from position 14868 relative
to the human sequence

NEQ a - north-eastern Queensland, individual C 564
NEQ b - north-eastern Queensland, individual Ps 7
MQ - middle eastern Queensland, individual C 529
SE a - south-eastern Queensland, individual Ps 1
SE b - eastern New South Wales, individual C 291
SE c - eastern New South Wales, individual L 226

                                                    Leu Ile Thr Gln Ile Ile Thr Gly Leu Leu Leu Ala Met His Tyr Thr
NEQ a                                                     C ACA CAA ATC ATC ACA GGC CTC CTC CTA GCC ATA CAT TAC ACA
NEQ b                                               CTA GT. ... ... ... ... ... ... ..T ... ... ... ... ... ... ...
MQ                                                  ... ... ... ... ... ..T ... ... ..T ... ... ... ..G ... ... ...
SE a                                                ... ... ... ... ... ..T ... ... ..T ... ... ... ..G ... ... ...
SE b                                                ... A.. ... ... ... ... ... ... ..T ... ... ... ..G ... ... ...
SE c                                                ... ... ... ... ... ... ... ... ..T ... ... ... ... ... ... ...

                                Ala Asp Thr Asn Leu Ala Phe Ser Ser Val Ala His Met Cys Arg Asn Val Gln Phe Gly Trp
NEQ a                           GCA GAC ACC AAC CTA GCC TTC TCC TCT GTA GCC CAC ATA TGC CGA AAT GTA CAA TTC GGA TGA
NEQ b                           ... ... ... .C. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
MQ                              ... ... ... .C. ... ... ... ... ..C ... ... ... ... ... ... ..C ... ... ... ... ...
SE a                            ... ... ... .C. ... ... ... ... ..C ... ... ... ... ... ... ..C ... ... ... ... ...
SE b                            ... ... ... .C. ... ... ... ... ..C ... ... ... ... ... ... ..C ... ... ... ... ...
SE c                            ... ... ... .C. ... ... ... ... ..C ... ... ... ... ... ... ..C ... ... ... ... ...

                                Leu Ile Arg Asn Leu His Ala Asn Gly Ala Ser Phe Phe Phe Ile Cys Ile Tyr Phe His Ile
NEQ a                           CTA ATC CGA AAC CTA CAT GCA AAC GGA GCT TCA TTC TTC TTC ATT TGT ATC TAC TTC CAC ATT
NEQ b                           ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
MQ                              ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SE a                            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SE b                            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SE c                            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
                                Gly Arg Gly Ile Tyr Tyr Gly Ser Tyr Leu Asn Lys Glu Thr Trp Asn Val Gly Val Ile Leu
NEQ a                           GGA CGA GGA ATC TAC TAC GGA TCA TAC CTA AAC AAA GAA ACC TGA AAC GTC GGA GTC AT
NEQ b                           ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ..
MQ                              ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ..C CTC
SE a                            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SE b                            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
SE c                            ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...

                                Leu Leu Thr Leu Met Ala Thr Ala Ser
MQ                              CTA CTA ACC CTC ATG GCA ACT GCT TCG
SE a                            ... ... ... ... ... ... ... ... .
SE b                            ... ... G.. ... ... ... ...
SE c                            ... ... ... ... ... ... ...
```

FIG. 7. Sequence of part of the cytochrome *b* gene in the Eastern Whipbird in individuals from NEQ, MQ and SE.

Taudactylus spp. and leaf-tailed geckos *Phyllurus* spp.) or those with representatives in the rainforests of all major eastern Australian rainforest blocks (e.g. the White-throated Treecreeper and Brown Thornbill complexes) are likely to be especially fruitful.

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APPENDIX 1. Restriction site matrix for the Large-billed Scrubwren.

Appendix 1. Matrix of restriction sites from RFLP data in the Large-billed Scrubwren *Sericornis magnirostris*. a - haplotype 1 - individuals SM2, 59, 60, 68; b - SM 71; c - SM1; d SM 66; e - SM75; f - SM 79; g - SM105; SF32 - *Sericornis frontalis* a - dare from south-eastern Queensland; e is from middle eastern Queensland; f and g are from north-eastern Queensland.

	Ava I	*Bam* HI	*Bcl* I	*Bgl* II	*Dra* I	*Eco* RI	*Eco* RV	*Nhe* I	*Pvu* II	*Sac* II	*Hind* III
a	1111110	111010000	111100	1100	1111	110	1	1100	1011000	11	111111100
b	1111110	111000000	111100	1100	1111	111	1	1100	1111100	11	111111100
c	1111110	111010000	111100	1100	1111	111	1	1100	1111100	11	111111100
d	1111110	111000000	111100	1100	1111	110	1	1100	1011000	11	111111100
e	1111110	111011000	111100	1100	1111	111	1	1100	1111100	11	111111100
f	1111100	111101000	101100	1000	1111	110	1	1110	1011000	11	111111100
g	1101100	111101000	101100	1000	1111	110	1	1110	1011000	11	111111101
SF32	1111101	110000111	000011	0011	1110	111	0	1001	0000011	11	111100010

APPENDIX 2. Restriction site matrix for the Eastern Whipbird.

Appendix 2. Matrix of restriction sites from RFLP data in the Eastern Whipbird *Psophodes olivaceus*. a - haplotype 1 field collection numbers D750, L226 (NSW); b - L255 (NSW); c - B840, C291 (NSW); d - Ps1 (SE Qld) and C529 (MQ); e- C564 (NE Qld)

	*Ava*I	*Bam* HI	*Bcl* I	*Bgl* II	*Dra* I	*Eco* 0109	*Eco* RI	*Eco* RV	*Hind* III	*Nco* I	*Nhe* I	*Pvu* II
a	11111	110111	101111	101	11111	10101	1110111	11	111111	10101	111	1111
b	11111	110111	101111	101	11111	10101	1110111	11	101111	10101	111	1111
c	11111	110111	101111	101	10101	10111	1110111	11	111111	11101	111	1011
d	11111	111111	111111	101	10101	10111	1110111	11	111111	10111	111	1111
e	11111	111111	101100	111	10111	11101	1111111	11	111011	01101	101	0110